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A refined chronology of prehistoric Madagascar and the demise of the megafauna

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ABSTRACT

The vertebrate community of Madagascar is one of the most unique and diverse on Earth, yet faunal diversity today is just a fraction of that present in the Pleistocene and Early Holocene. An understanding of the chronology of extinction relative to climate change and anthropogenic factors is essential to test hypotheses for extinction. Here, I combine over 200 new radiocarbon dates with published ^{14}C dates from extinct and extant subfossil vertebrates. These new data provide evidence for the prolonged existence of both extant and extinct endemic terrestrial vertebrate species well before human arrival, with habitation of some localities extending back before the Last Glacial Maximum. I analyze the data for patterns among body sizes and ecoregions in relation to four major historical events: human arrival (ca 2500 years ago), establishment of human settlements (ca 1500 years ago), Late Holocene aridification (peaking ca 1000 years ago), and European arrival (ca 500 years ago). Patterns in endemic species abundance after human arrival differ depending on body size and geographic location. Within the first 500 years after human arrival, there were population declines in (1) very large species (>150 kg) and large species (10–150 kg) in the Dry Deciduous Forest, (2) large species in the Central Highlands, and (3) very large species in the Spiny Thicket. This first pulse of declines was likely triggered by human predation. Large species continued to be well represented in the Spiny Thicket and Succulent Woodland until ca 1000 years ago, when their populations plummeted. This second pulse of declines may have been solely triggered by continued human predation, or it may have resulted from a combination of increasing Late Holocene aridity and human impacts in the form of hunting and habitat modification. The abundance of endemic animals weighing <10 kg increased dramatically in the aftermath of the decline in large-bodied species.

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1. Introduction

Madagascar is home to some of the most unique animals on Earth (Goodman, 1999). Our knowledge of this diverse radiation, which included numerous now extinct taxa, is limited to the Late Quaternary. Elephant birds, giant tortoises, pygmy hippopotamuses, and a diverse radiation of large lemurs coexisted with a range of other species that survived to the present day. Yet the extent of ecological overlap among species is scarcely known, in part because radiocarbon dates for subfossil[1] species are few. A Holocene fossil record that is largely devoid of temporal context is one of the greatest obstacles to understanding the ecology and extinction of Madagascar's megafauna.

All endemic species >10 kg, including at least 17 species of lemur, are extinct (Burney and MacPhee, 1988). At least six hypotheses have been proposed to explain this mass extinction. One directly implicates environmental change in the form of aridification (Mahé and Sourdat, 1972), whereas the others invoke anthropogenic changes over the past 2500 years. These include over-hunting (Walker, 1967), competition with introduced wild and domestic animals (Dewar, 1984), introduced hypervirulent diseases (MacPhee and Marx, 1997), habitat loss associated with fire (Humbert, 1927), or a synergistic combination of environmental and anthropogenic factors (Burney and MacPhee, 1988; Burney, 1999). This latter view has since achieved widespread acceptance (MacPhee and Burney, 1991; Burney, 1993, 1999; Simons et al., 1995; Burney et al., 1997, 2003, 2004; Godfrey and Jungers, 2003; Clarke et al., 2006; Godfrey and Irwin, 2007; Virah-Sawmy et al., 2009, 2010), although authors place differing emphasis on which of the factors were most important.

Tests of these hypotheses are difficult without more precise data concerning the timing of the demise of various extinct species. In the most comprehensive survey to date, Burney et al. (2004) evaluated

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[1] The term "subfossil" is used because the bones still contain substantial amounts of protein, are not completely recrystallized, and do not have pores that are filled with diagenetic minerals.

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archaeological, paleontological, and palynological data from the Late Quaternary. Their analysis suggested that with the exception of *Babakotia radofilai* (an extinct sloth lemur known from a limited number of specimens and only one radiocarbon date), all extinct animal taxa were present when humans arrived ca 2500 years before present (BP[2]), with some persisting as recently as 500 years BP. Such an implied protracted co-existence with humans is at odds with a rapid pulse of extinction due to island-wide large-scale fires, hypervirulent pandemic disease, or blitzkrieg over-hunting (sensu Martin, 1984). Similarly, there is little evidence that climate change could have been solely responsible. While there is evidence for island-wide aridification ca 1000 Cal BP, there was nothing exceptional about the degree of Late Holocene desiccation, and dramatic climate fluctuations throughout the Pleistocene did not result in any known extinctions (Burney, 1993; Gasse and Van Campo, 1998, 2001; Virah-Sawmy et al., 2009). Finally, competition with introduced species seems an unlikely cause of the extinctions by itself. Some species, such as rats may have arrived with the first humans (Vasey and Burney, 2007). It is assumed (but unconfirmed) that Predatory Indian civets (*Viverricula indica*), and domestic cats and dogs also arrived with the first wave of human colonizers (Garbutt, 2007), however, their presence was not documented until ca 350 years ago (de Flacourt, 1661). Larger domestic species such as cattle probably arrived after ca 1000 Cal BP (Burney et al., 2003).

While it is possible that low levels of hunting pressure, increasing hunting pressure over several centuries, or a combination of anthropogenic and climatic pressures resulted in the demise of the extinct species, limited radiocarbon data have hindered identifying patterns in species decline.

Large temporal and spatial gaps remain in the previously published record of the biochronology of Madagascar. It is unknown if some species declined before others, or if there were any spatial patterns in decline. Here I present 209 new radiometric ^{14}C dates from terrestrial vertebrate bones collected from Late Pleistocene and Holocene localities across Madagascar, and combine these dates with previously published dates for 97 Madagascan vertebrates (Burney et al., 2004, 2008; Karanth et al., 2005; Perez et al., 2005; Clarke et al., 2006; Samonds et al., in press; Muldoon et al., 2009) (Fig. 1; Table 1; Appendix A). This combined dataset provides an unprecedented degree of temporal and spatial resolution. In particular, it permits an examination of how extinct species responded to key episodes during the past 2500 years, including initial human colonization, expanding human settlement, European contact, and Late Holocene aridification (Fig. 2). These new dates augment the work of previous researchers and advance our understanding of the prehistoric chronology of Madagascar. The results impact not merely our understanding of recent palaeoecological changes in Madagascar, but also help to better evaluate the causes of megafaunal extinctions.

2. Regional setting

Based on modern floristic and rainfall patterns, Madagascar has been divided into seven ecogeographic zones (Burgess et al., 2004; Fig. 1). Mean annual temperature is fairly constant across the island (Burgess et al., 2004). Temperatures are highest along the coast and decline inland with an altitudinal lapse rate of roughly 1.5°C/305 m (Tattersall and Sussman, 1975; Goodman and Benstead, 2003; Burgess et al., 2004). Aridity and seasonality of rainfall, however, tend to increase from the north to the south and from the east to the west. These trends derive largely from elevation differences, and a rainshadow effect associated with the mountain range

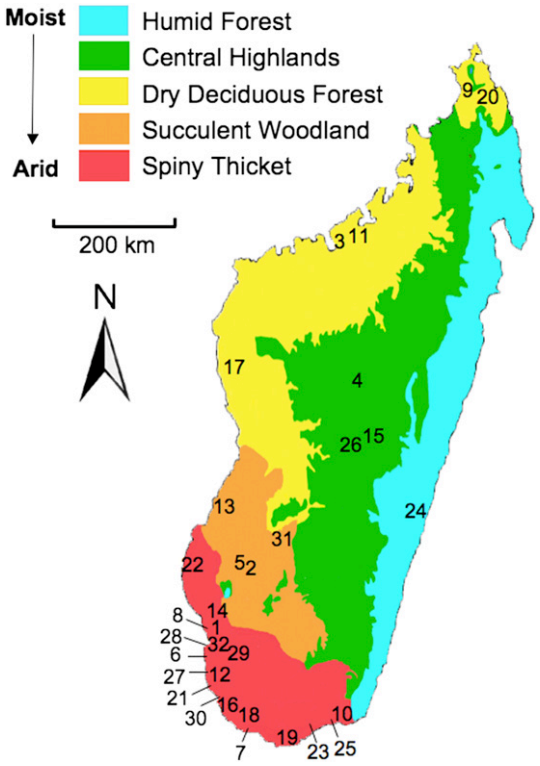

Fig. 1. Distribution of subfossil localities in Madagascar. Phytogeographic ecoregions are adapted from Cornet (1974); Burgess et al. (2004). Mangrove and ericoid thicket ecoregions are not included because they are small in extent and do not contain subfossil localities. Numbered subfossil localities are identified in Table 1.

that runs from the north to the south, dividing Madagascar into eastern and western sections. Precipitation from the trade winds preferentially falls on eastern Madagascar; however seasonal cyclones bring moisture to the more arid regions. Whereas the Humid Forest Ecoregion along the east coast of Madagascar has abundant precipitation and little to no dry season, the Spiny Thicket, Succulent Woodland, and Dry Deciduous Forest ecoregions in the west and southwest are characterized by extreme aridity and seasonality of rainfall.

2.1. Subfossil localities

The Pleistocene subfossil record is sparse. With the exception of limited data from a handful of localities, the Ankarana in the north (Simons et al., 1995), Anjohibe in the northwest (Samonds, 2007), and Ampasambazimba in the Central Highlands (this paper), nothing is known of Pleistocene faunal communities. The Holocene record is much more robust, but subfossil localities are not equally distributed across the island. While southwestern Madagascar contains dozens of localities, localities in the northern and central parts of the island are more rare, and eastern Madagascar has just one described locality (Burney et al., 2004; Fig. 1; Table 1). These differences result mainly from differences in preservation potential across ecoregions; the dry conditions in the west are far superior to the moist forests of the east for preserving the organic portions of bone. Nevertheless, it is also likely that there were true differences in the relative abundance or carrying capacity of animals in each ecoregion prior to human arrival. Early spore counts for the dung fungus *Sporormiella*, which serves as a proxy for large animal biomass, were also highest in southwestern Madagascar, more moderate in the Central Highlands and minimal in the humid areas in the east prior to human arrival (Burney et al., 2003).

[2] Throughout the text I will refer to conventional ^{14}C radiocarbon years (^{14}C BP) and calibrated calendar ^{14}C years (Cal BP). See the Methods for further details.

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Table 1
Geographic coordinates and depositional environment for localities with subfossil bones that have yielded ^{14}C dates. Map numbers correspond to numbered localities in Fig. 1.

Map #	Locality	Lat (°S)	Long (°E)	Depositional environment
1	Ampamalora	23.07	43.75	Coastal Dunes
2	Ampanihy	22.32	44.70	Flood Plain
3	Amparihingidro	15.73	46.35	Coastal Lake
4	Ampasambazimba (Itasy)	18.90	46.73	Paleolake/Wetland
5	Ampoza	22.32	44.73	Flood Plain
6	Anakao	23.65	43.65	Coastal Dunes
7	Anavoha (Beloha)	25.17	45.05	Coastal Dunes
8	Andolonomby	23.07	43.75	Hypersaline Coastal Pond
9	Ansiroandoha/Andrafiabe[a]	12.90	49.08	Cave
10	Andrahomana[b]	25.20	46.63	Coastal Cave
11	Anjohibe/Anjohikely/ Lavakasaka[a]	15.55	46.89	Cave
12	Ankazoabo Grotte	24.55	43.93	Cave
13	Belo Sur Mer (Ankilibehandry)	20.73	44.02	Interdunal Swale
14	Ankilitelo	22.90	43.87	Pit Cave
15	Antsirabe	19.87	47.03	Paleolake/Wetland
16	Bemafandry	24.98	44.12	Coastal Dunes
17	Bemaraha[c]	18.0	45.0	Limestone Karst
18	Bevoha	25.07	44.32	Coastal Dunes
19	Faux Cap	25.55	45.53	Coastal Dunes
20	Irodo (Tafiantsirbeka)	12.63	49.52	Coastal Dunes
21	Itampolo	24.68	43.95	Interdunal Swale
22	Lamboharana	22.20	43.23	Shallow Pond
23	Manambovo	25.47	45.70	River Mouth
24	Mananjary[d]	21.23	48.03	Flood Plain
25	Maroaloke	25.20	46.20	Coastal Dunes
26	Masinandraina	19.85	47.07	Large Wetland
27	Mitoho	24.05	43.77	Cave
	Southern Madagascar[e]	19.00	47.00	
28	SW Madagascar, near Nosy Ve[d]	23.62	43.58	
29	Taolambiby	23.67	44.42	Seepage Deposit
30	Tsiandroina	24.98	44.12	Coastal Lake
31	Tsirave	21.83	45.12	Open Air Deposit. Possibly River Flood Plain
32	Tulear[c]	21.02	47.00	Coastal Dunes

[a] Coordinates are from Antsiroandoha, and Anjohibe respectively.
[b] Includes one specimen from "Fort Dauphin".
[c] Coordinates are approximate.
[d] Coordinates are approximate. Actual location is unknown.
[e] Locality is unknown. Coordinates recorded as 19°S, 47°E (Marden, 1967), but this is close to Antsirabe in the Central Highlands and not in southern Madagascar.

2.2. Climate during the Pleistocene and Holocene

Due to poor preservation of any Cenozoic fossil material until the Late Pleistocene, little is known about climate regimes throughout the Cenozoic or about the evolution of Madagascar's unique flora and fauna (Phillipson, 1996; Wells, 2003; Burney et al., 2004). It has been surmised that the island was affected by the commencement of cold ocean circulation around Antarctica at the end of the Oligocene, as well as more recent temperature and sea level changes associated with glacial–interglacial cycles throughout the Pleistocene, but hard evidence for variation in climate, vegetation, and faunal diversity only begins in the Late Pleistocene (Burney, 1997).

Cool and dry glacial conditions were prevalent starting at least ca 40 800 Cal BP[3] (Gasse and Van Campo, 1998). From 40 000–39 000, 37 000–32 400, and 22 700–16 900 Cal BP (the last glacial maximum), temperatures were exceptionally low (Gasse and Van Campo, 1998). Warm and moist conditions then prevailed starting ca 16 900 Cal BP and lasting into the Early Holocene (Gasse and Van Campo, 1998). The subfossil fauna attest to these moister climates; many localities in the west and southwest that are currently open grasslands, dried up lakes, or degraded ruderal vegetation have yielded the remains of forest-dwelling lemurs and aquatic birds (Battistini, 1971; Mahé and Sourdat, 1972; MacPhee et al., 1985; Burney, 1993, 1997; Goodman and Rakotozafy, 1997; Godfrey et al., 1999). Approximately 4600 Cal BP, there was a brief and intense drought (Gasse and Van Campo, 1998; Virah-Sawmy et al., 2009). Following this dry spell, moister conditions briefly returned. Then, starting around 3000 BP, aridification recommenced, with particularly pronounced effects in the southwest (Burney, 1993).

Since the Late Pleistocene, there have been considerable shifts in vegetation across Madagascar (Burney, 1987a,b, 1993; Matsumoto and Burney, 1994; Burney et al., 1997, 2004; Gasse and Van Campo, 1998; Virah-Sawmy et al., 2009). In general, vegetation changes were regional in scale. However, an island-wide transition towards more open vegetation, particularly grasses, at the expense of woody vegetation coincided with a peak in Late Holocene aridity ca 1300–950 Cal BP (Burney, 1987a,b; Burney, 1993; Matsumoto and Burney, 1994; Virah-Sawmy et al., 2009).

2.3. Human colonization

It is estimated that humans came to Madagascar from Indonesia or Africa before 2300 Cal BP (Perez et al., 2003; Tofanelli et al., 2009). Evidence of early human presence in the form of introduced *Cannabis* pollen, increased charcoal microparticles (suggesting an increase in the frequency or intensity of fire), and bones of extinct species bearing the signs of butchery in sediments occurs in southwestern Madagascar and along the western coastline ca 2300–1800 Cal BP (MacPhee and Burney, 1991; Burney, 1993; Parker Pearson et al., 2002; Perez et al., 2003). There is, however, no evidence for intensive human habitation in the southwest until 500–600 cal BP (Esoavelomandroso, 1995). Although *Cannabis* pollen is present in lake sediments ca 2200 Cal BP in the Central Highlands (Burney, 1987a; Gasse and Van Campo, 1998), charcoal levels in sediment cores suggest that interior parts of Madagascar did not have high human populations until roughly 1400 Cal BP (Burney, 1987a,c; Burney et al., 1997).

Clear evidence for human occupation and settlement in the north and northeast comes from cave deposits containing potsherds, the earliest of which dates to 1145 ± 145 Cal BP (Vérin, 1975; Dewar, 1984; Dewar and Rakotovololona, 1992; Dewar and Wright, 1993). However, charcoal records suggest that human activity in the northwest also intensified more recently, possibly 1000–500 Cal BP (Matsumoto and Burney, 1994; Burney et al., 1997). Large, urban-scale occupation sites (e.g. Mahilaka) on the northeast coast, which thrived from ca 1100 to 1300 Cal BP were established shortly after these smaller settlements (Radimilahy, 1997). Finally, human occupation sites in the southeast yield slightly more recent dates, 650 ± 120, 805 ± 145 Cal BP, respectively (Dewar and Wright, 1993). Similar to the southwest, anthropogenic activity was probably mild until approximately 500 Cal BP (Virah-Sawmy et al., 2009). This period of increased human activity in southern Madagascar coincided with the beginning of the European period, which commenced ca 500 years ago (Brown, 1978).

3. Materials and methods

3.1. Sample preparation

Collagenous extracts were obtained as described in Crowley et al. (2010). Approximately 200 mg of bone were collected from an assortment of fragmented museum specimens. Samples were decalcified in 0.5 M EDTA for 10 days at 10 °C, and 10 days at room temperature, rinsed 10x in ultra pure water, and gelatinized in

[3] These dates are approximate. These authors only present calibrated dates and they adopted a different calibration technique than the one I use in this manuscript.

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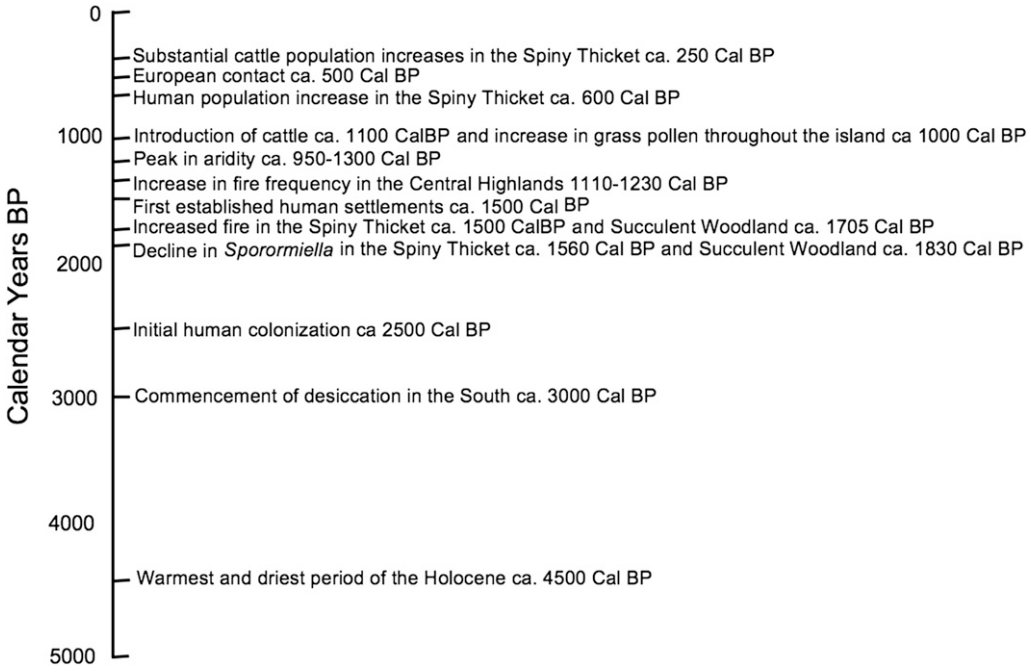
Calendar Years BP
0
1000
2000
3000
4000
5000
Substantial cattle population increases in the Spiny Thicket ca. 250 Cal BP
European contact ca. 500 Cal BP
Human population increase in the Spiny Thicket ca. 600 Cal BP
Introduction of cattle ca. 1100 CalBP and increase in grass pollen throughout the island ca 1000 Cal BP
Peak in aridity ca. 950-1300 Cal BP
Increase in fire frequency in the Central Highlands 1110-1230 Cal BP
First established human settlements ca. 1500 Cal BP
Increased fire in the Spiny Thicket ca. 1500 CalBP and Succulent Woodland ca. 1705 Cal BP
Decline in Sporormiella in the Spiny Thicket ca. 1560 Cal BP and Succulent Woodland ca. 1830 Cal BP
Initial human colonization ca 2500 Cal BP
Commencement of desiccation in the South ca. 3000 Cal BP
Warmest and driest period of the Holocene ca. 4500 Cal BP

Fig. 2. Timeline of events in Madagascar over the past 5000 years (Cal BP). Sources: Burney, 1987a,b, 1993; MacPhee and Burney 1991; Dewar and Rakotovololona, 1992; Dewar and Wright, 1993; Matsumoto and Burney, 1994; Esoavelomandroso, 1995; Gasse and Van Campo, 1998; Burney et al., 2003, 2004; Kaufmann, 2004; Virah-Sawmy et al., 2009.

0.01 N HCl at 57 °C. Collagenous residues were then filtered using a 1.5 μm glass-fiber filter and dried under vacuum. Collagen integrity was determined by analyzing samples on a Thermo-Electron (Finnigan) Delta + XP continuous flow system connected to an Elemental Analyzer at the University of California, Santa Cruz Stable Isotope Laboratory, and verifying acceptable atomic C:N ratios, stable isotope values, and collagen yield (Ambrose, 1990). Samples with marginally acceptable C:N ratios were ultrafiltered using pre-cleaned Centriprep ultrafilters (Higham et al., 2006), with retention and lyophilization of the >30 kDa fraction. C:N ratios were then reanalyzed on the Elemental Analyzer.

Radiocarbon dates were obtained at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory. Conventional radiocarbon age estimates are based on a 5568 year half-life, ^{13}C-corrected, and include a background subtraction based on simultaneously prepared modern and ^{14}C-free bone standards. I compiled additional ^{14}C data from the literature (Burney et al., 2004, 2008; Karanth et al., 2005; Perez et al., 2005; Clarke et al., 2006; Samonds et al., in press; Muldoon et al., 2009; see Appendix A for details). As noted by Burney et al. (2004), although it is unclear whether or not many dates from the literature have been corrected for δ^{13}C isotopic fractionation, correction of these dates would change them only very slightly. I omitted three published dates from my analysis: one from dung attributed to a young *Archaeolemur* sp. cf. *edwardsi* at Anjohikely in the Dry Deciduous Forest (Burney et al., 1997), and two from a hippo skull ostensibly from Mananjary in the Humid Forest (Burney et al., 2004). The dung was omitted because I only included dated animal tissues in my analysis. The hippo was omitted because its provenience is questionable. This skull may have been brought to Madagascar from Africa as a comparative specimen (L.R. Godfrey, personal communication). There is no published record of it having been found at Mananjary, and no specimen number associated with the skull.

3.2. Data analyses

Using a 20-year moving average, I calibrated individual and mean ages to calendar years BP (Cal BP) in Calib 5.01 (Stuiver and Reimer, 1993). Samples with radiocarbon ages younger than 11 000 BP were calibrated using the Southern Hemisphere calibration curve SHCal (McCormac et al., 2004). Ages between 11 000 and 26 000 BP were corrected for the average 56 ± 24 year time lag between the Northern and Southern Hemispheres, the offset error was added to sample error in quadrature (McCormac et al., 2004), and the corrected dates and errors were then calibrated using IntCal04 (Reimer et al., 2004). I rounded all calibrated ages to the nearest 10 years. Because no agreed upon calibration curve exists for radiocarbon ages >26 000 BP (Reimer et al., 2004), I present the oldest dates as uncalibrated conventional ^{14}C ages BP (^{14}C BP).

I examined the relationship between body mass and age using Pearson's χ^2 test (Table 3, α set at 0.05). I grouped animals into three body mass categories (small-to-medium, <10 kg; large, 10–150 kg, and very large, >150 kg) (following Amadon, 1947; Grubb, 1971; MacPhee, 1994; Goodman et al., 2004; Garbutt, 2007; Jungers et al., 2008), and initially used six age categories (0–500, 500–1000, 1000–1500,1500–2000, 2000–2500, and >2500 Cal BP). The very large body mass group (>150 kg), composed entirely of extinct genera, includes *Hippopotamus*, *Geochelone* (tortoises), *Aepyornis* and *Mullerornis* (elephant birds), and *Archaeoindris*, a lemur. The large body size group (10–150 kg), also composed entirely of extinct taxa, is dominated by primate genera (*Archaeolemur*, *Babakotia*, *Hadropithecus*, *Megaladapis*, *Mesopropithecus*, *Pachylemur*, and *Palaeopropithecus*), an extinct species of *Daubentonia*, the enigmatic, aardvark-like bibymalagasid *Plesiorycteropus*, and the euplerid carnivore *Cryptoprocta spelea*. The small-to-medium body mass group (<10 kg) encompasses several extant lemur genera (*Eulemur, Hapalemur, Indri, Lemur, Microcebus, Propithecus*), a bat (*Eidolon dupreanum*), rodents (*Hypogeomys*[4] and *Macrotarsomys*), a euplerid carnivore (*Fossa fossana*), a tenrecid (*Tenrec ecaudatus*), and two extinct birds (*Alopochen sirabensis* and *Centrornis majori*).

[4] My *Hypogeomys* sample may include both *H. australis* (extinct) and *H. antimena* (extant).

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I then used Pearson's χ^2 test to compare frequencies of dates in the various time periods across ecoregions (Table 4, α set at 0.05). Due to sample size limitations, I reduced the number of age categories (0–1000, 1000–2500, and >2500 Cal BP), and lumped very large (>150 kg) and large species (10–150 kg). Additionally, I combined dates from the Spiny Thicket and Succulent Woodland; whereas some researchers recognize these two ecoregions as separate (mainly based on precipitation differences, e.g. Burgess et al., 2004; Muldoon and Simons, 2007), others have lumped them based on similarities in tree genera and levels of endemism (Schatz, 2000; Wilmé et al., 2006; Vences et al., 2009). Finally, I used Pearson's χ^2 test to examine the relationship between body and age just in the southwest (Table 5, α set at 0.05).

Radiocarbon data are inherently patchy, and it is highly improbable that the last surviving member of a species will be excavated and dated (McFarlane, 1999; Haile et al., 2009). Consequently, even with a dataset of over 300 radiocarbon dates, I can only examine patterns in the decline of the extinct species. It is not possible to say with assurance when they finally disappeared. However, it is possible to place more certainty on extinction dates by applying confidence intervals (CI) around measured dates (e.g. Strauss and Sadler, 1989; Marshall, 1991; McFarlane, 1999; Haile et al., 2009). Confidence intervals provide a way of confirming sudden extinction events and determining how far above the most recent ^{14}C date the actual extinction may have occurred.

I calculated upper 50% CI for radiocarbon ages for each body mass group in each ecoregion using the method developed by Strauss and Sadler (1989):

$$r/R = (1 - C_1)^{-1/(H-1)} - 1 \quad (1)$$

Where r is the size of the confidence interval (e.g. 50%), R is the observed temporal range, C_1 is the upper confidence interval in calendar years, and H is the number of known dates for each group. I chose 50% CI because they 95% CI are far too conservative for the number of dates I have to work with (C.R. Marshal, personal communication). I did not use the entire subfossil ^{14}C dataset to calculate CI; I only used specimens 0–4000 Cal BP. I chose 4000 Cal BP as a cutoff for two reasons. First, I could not use the entire dataset because CI calculations require normally distributed data (Strauss and Sadler, 1989; Marshall, 1991). Although some radiocarbon dates extend back into the Pleistocene, the majority of the dates are relatively recent, with a mean age of 2757 ^{14}C BP (2760–2850 Cal BP). Using a 4000 Cal BP cutoff normalizes the data and only removes 17% (54 out of 322) of the dated samples. Additionally, 4000 Cal BP is within the 90% Quantile (4868 ^{14}C BP) and well outside the lower 95% confidence interval (3126 ^{14}C BP) for all endemic taxa. Second, depositional environments shifted between the Late Pleistocene and the Late Holocene. 4000 Cal BP follows the peak in mid Holocene aridity and is close to the transition towards Late Holocene climatic conditions (Burney, 1993; Gasse and Van Campo, 1998; Virah-Sawmy et al., 2009).

I also estimated the probability (P) that each group was present 1000 Cal BP, 500 Cal BP, and 0 BP for each group:

$$P = (1 + r/R)^{(H-1)} \quad (2)$$

where r, R and H are the same as in Equation (1), and $P = 1 - C_1$. Statistical analyses were performed using JMP 7.0 and Minitab 15.

4. Results

Taxonomic identification, conventional and calibrated ^{14}C ages, preparation methods (if known), and data sources for each specimen are presented in Appendix A. Overall, the number of dated occurrences for very large taxa is small compared to the number of dated occurrences for large and small-to-medium-bodied taxa. With the exception of *Babakotia radofilai*, and *Centrornis majori*, which each have only one radiocarbon date, all of the known recently extinct species are known to have persisted through climate and vegetation changes during the Pleistocene and Early Holocene, and were still present when humans arrived ca 2500 Cal BP. New ^{14}C dates span almost 30 000 years for endemic taxa (Fig. 3; Appendix A). Conversely, radiocarbon dates for introduced taxa are modern, or close to modern (Table 2). Only a handful of bones from a limited number of introduced species have been dated, and no dates exist for domesticated livestock.

When combined with published dates, there is a significant relationship between radiocarbon age and body mass for endemic vertebrates ($\chi^2 = 93.30$, $n = 322$, df = 10, $p < 0.0001$). For very large animals (>150 kg), the observed number of dates is higher than expected before 2500 Cal BP, and between 2000 and 2500 Cal BP. Observed and expected values are nearly identical between 1500 and 2000 Cal BP, but the observed value drops to considerably lower than expected after 1500 Cal BP (Table 3). For large animals (10–150 kg), the observed frequencies are similar to or higher than expected prior to 1000 Cal BP. However, observed frequencies are lower than expected between 500 and 1000 Cal BP, and much lower than expected 0–500 Cal BP. For small-to-medium-bodied animals (<10 kg), observed frequencies are lower than expected prior to 1500 Cal BP, similar to expected from 1000 to 1500 Cal BP, and then higher than expected more recently than 1000 BP (Table 3). This pattern suggests that populations of very large animals declined first, followed by populations of large animals (including most of the extinct primates). However, it is important to note that overall, the number of dated occurrences for very large taxa is small compared to the number of dated occurrences for large and small-to-medium-bodied taxa.

There are also geographic patterns in species decline. For endemic taxa >10 kg (i.e., large and very large animals), there is a significant relationship between radiocarbon age and geographic location (ecoregion) ($\chi^2 = 25.74$, $n = 221$, df = 4, $p < 0.0001$). Between 1000 and 2500 Cal BP, observed frequencies are similar to expected in the Spiny Thicket/Succulent Woodland, but lower than expected in both the Central Highlands and the Dry Deciduous Forest (Table 4). The drop in abundance of taxa >10 kg in the southwest only emerges after 1000 Cal BP (Table 4).

The prolonged persistence of extinct species in the southwest allowed for a more detailed examination of patterns in decline among different body sizes in this region. Again, sample limitations required lumping of 500-year time bins. In order to identify any early declines, I created four age categories: 0–1000, 1000–2000, 2000–2500, and >2500 Cal BP. There is a significant relationship between radiocarbon age and body size ($\chi^2 = 78.87$, $n = 232$, df = 6, $p < 0.0001$). The observed frequencies of very large species are greater than expected before 2000 Cal BP, but less than expected after 2000 Cal BP (Table 5). Conversely, the observed frequencies for large species are similar to or greater than expected frequencies until 1000 Cal BP, when their observed frequencies drop dramatically (Table 5). Observed frequencies for endemic small-to-medium-bodied species are lower than expected before 2000 Cal BP, similar to expected between 1000 and 2000 Cal BP, and much greater than expected between 0 and 1000 Cal BP.

Based on the χ^2 results, patterns in species decline emerge. Frequency data suggest that island-wide, very large taxa were affected within 1000 years after human arrival and large taxa persisted for an additional 500 years. Additionally, frequency data suggest that small-to-medium-sized taxa declined early in the Central Highlands. However, χ^2 results are hampered by sample size limitations. Visual inspection of the data reveals additional trends that are not apparent in the χ^2 analyses.

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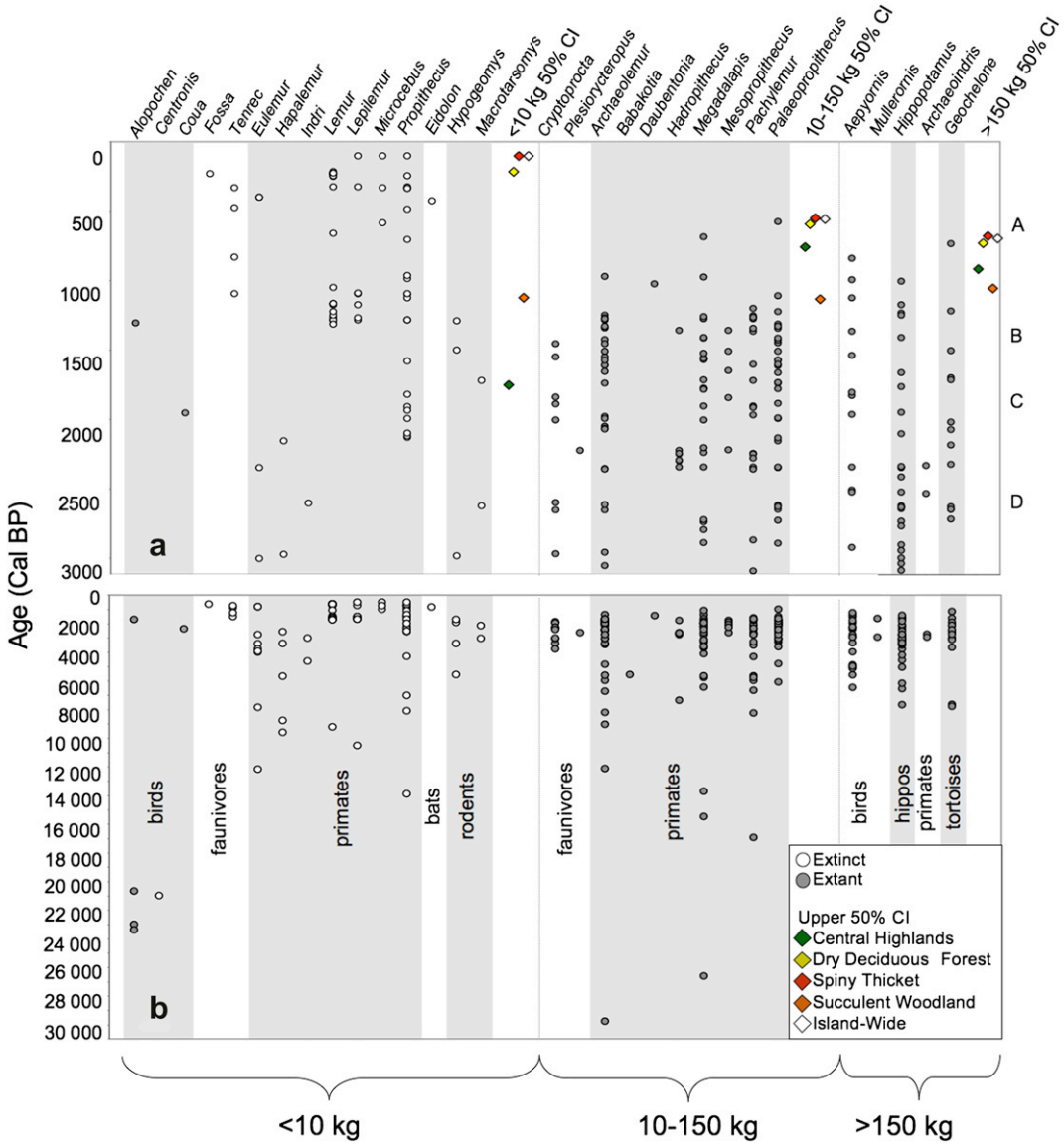

Fig. 3. Scatterplots showing the subset of ^{14}C dates for subfossil endemic genera from 0 to 3000 BP and 50% confidence intervals for each body mass group (a), and all radiocarbon dates (b). White and grey circles identify extant and extinct taxa, respectively. Due to calibration constraints, dates >22 000 years are presented in uncalibrated conventional ^{14}C years before present (^{14}C BP). An eggshell from *Aepyornis* sp. deemed too old to carbon date (Clarke et al., 2006) was not included. Letters correspond to European contact (A), the peak in Late Holocene aridity (B), first large human settlements (C), and initial human colonization (D).

Table 2
Radiocarbon dates for introduced species.

Taxon	Specimen no.	Ecoregion	Mean ^{14}C age	$\pm1\sigma$	Mean cal age	$\pm1\sigma$
Canis familiaris	uncatalogued	Spiny Thicket	Modern		Modern	
C. familiaris	AM 7067	Spiny Thicket	145	30	135	135
C. familiaris	AM 7065	Succulent Woodland	155	30	140	140
Felis domesticus	uncatalogued	Spiny Thicket	Modern		Modern	
Rattus rattus	A-86-200 (UM)	Dry Deciduous Forest	Modern		Modern	
Rattus rattus	A-86-200 (UM)	Dry Deciduous Forest	Modern		Modern	
Numida meleagris	UA-322	Central Highlands	90	60	140	140

In agreement with the χ^2 results, dated occurrences for both very large and large species declined by 2000 Cal BP in the Dry Deciduous Forest, and dated occurrences for small-to-medium-bodied species increased in the last 500 years (Fig. 4). Dated occurrences for very large species in the Spiny Thicket also declined by 2000 Cal BP, and in agreement with χ^2 results, the number of occurrences for large species remained stable until ca 1000 Cal BP. The number of small-to-medium-bodied species increased in the Spiny Thicket starting ca 1500 Cal BP. The pattern in the Succulent Woodland is slightly different. The number of dated occurrences for both very large and large species remained stable until ca 1000 Cal BP. Dated occurrences for small-to-medium-bodied species increased between 1000 and 2000 Cal BP, but there are no dates for such species after 1000 Cal BP (Fig. 4). Patterns for the Central Highlands also differ slightly from the χ^2 results; small-to-medium-sized and large species declined between 2000 and 2500 Cal BP, and the abundance of very large taxa remained low and relatively stable until ca 1000 Cal BP (Fig. 4).

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Table 3
Contingency table from χ^2 analysis illustrating the relationship between body mass and calibrated age. The χ^2 contribution refers to the amount each cell contributes to the total χ^2 statistic (93.30).

Group	>2500	2500–2000	2000–1500	1500–1000	1000–500	500-present	Total
<10 kg							
Observed	26	4	7	25	6	30	98
Expected	33.2	12.2	15.5	23.7	4	9.4	
χ^2 Contribution	1.6	5.5	4.7	0.1	1.1	44.8	
10–150 kg							
Observed	49	23	34	43	4	1	154
Expected	52.1	19.1	24.4	34.3	6.2	14.8	
χ^2 Contribution	0.2	0.8	3.8	0.9	0.8	12.9	
>150 kg							
Observed	34	13	10	10	3	0	70
Expected	23.7	8.7	11.1	17	2.8	6.7	
χ^2 Contribution	4.5	2.1	0.1	2.9	0.01	6.7	
Total	109	40	51	78	13	31	322

50% confidence intervals (CI) for each mass group in each ecoregion yield additional temporal information (Fig. 3, Table 7). The largest calculated 50% CI are for very large animals in the Central Highlands, Dry Deciduous Forest and Succulent Woodland, and large animals in the Central Highlands and Dry Deciduous Forest (Table 7). These are groups with poor records (<10 dates). Aside from these groups, 50% confidence intervals are small, <160 calendar years. In general, CI suggest that extinct species persisted beyond the last dated occurrences. Nevertheless, CI corroborate the patterns in species decline predicted from χ^2 analyses. Although it is almost certain that extinct large and very large animals were still present in all ecoregions 1000 years ago, confidence intervals suggest that the likelihood of finding the remains of an extinct species that is 500 years old are slimmer (≤50%), and there is virtually no chance of finding a relatively modern bone.

5. Discussion

Here I report the most comprehensive collection of radiometric dates from Madagascan vertebrates. A diverse array of extinct very large and large animals is known to have occupied nearly all ecoregions in Madagascar during the Late Quaternary (e.g. Godfrey et al., 1997; Hawkins and Goodman, 2003). I determine that such widespread occurrences still existed when human colonization commenced. However, within 500 years after initial human colonization (ca 2500 Cal BP) radiocarbon dates reveal declines 1) in very large species in the Dry Deciduous Forest and the Spiny Thicket, 2) in large extinct species in the Central Highlands and the Dry Deciduous Forest, and 3) in small-to-medium-bodied species in the Central Highlands (Fig. 4). Dated occurrences for large species remain high in the Spiny Thicket and Succulent Woodland until ca 1000 Cal BP. The tempo of decline and disappearance among numerous large-bodied taxa in different ecoregions sheds light on the factors that may have resulted in the extinction of such animals.

5.1. Reevaluating extinction hypotheses

The initial wave of population declines in the Central Highlands, Dry Deciduous Forest, and Spiny Thicket predates the establishment of large human settlements, widespread fire, the introduction of livestock, and the peak in Late Holocene aridity (Fig. 2 through 4) (Burney, 1987a,b; Burney, 1993; Matsumoto and Burney, 1994; Burney et al., 2003; Virah-Sawmy et al., 2009), indicating that such factors played a limited role in the disappearance of the large-bodied taxa. Moreover, the size-biased pattern of decline is inconsistent with the hypervirulence hypothesis, which predicts that all size classes should decline synchronously (MacPhee and Marx, 1997).

Instead, these declines are consistent with the predictions of hunting as an initial trigger (Walker, 1967; Martin, 1984; Burney and MacPhee, 1988; Godfrey and Irwin, 2007). In the absence of any other known cause for island-wide population decreases in

Table 4
Contingency table from χ^2 analysis illustrating the relationship between ecoregion and calibrated age for all endemic vertebrates >10 kg. The χ^2 contribution refers to the amount each cell contributes to the total χ^2 statistic (25.74). Note that although two cells in the contingency table have expected counts less than five, the χ^2 result is still highly significant if I allow for a reduction in the degrees of freedom.

Group	>2500	1000–2500	0–1000	Total
Central Highlands				
Observed	18	10	1	29
Expected	10.9	17.1	1	
χ^2 Contribution	4.6	2.9	0.002	
Dry Deciduous Forest				
Observed	15	4	1	20
Expected	7.5	11.8	0.7	
χ^2 Contribution	7.5	5.1	0.1	
Spiny Thicket and Succulent Woodland				
Observed	50	116	6	172
Expected	64.6	101.2	6.2	
χ^2 Contribution	3.3	2.8	0.01	
Total	83	130	8	221

Table 5
Contingency table from χ^2 analysis illustrating the relationship between body mass and calibrated age for all endemic vertebrates from the southwest. The χ^2 contribution refers to the amount each cell contributes to the total χ^2 statistic (78.87).

Group	>2500	2000–2500	1000–2000	0–1000	Total
<10 kg					
Observed	4	1	31	24	60
Expected	14	8	30.3	7.8	
χ^2 Contribution	7.1	6.1	0	34	
10–150 kg					
Observed	26	21	70	3	120
Expected	27.9	16	60.5	15.5	
χ^2 Contribution	0.1	1.5	1.5	10.1	
>150 kg					
Observed	24	9	16	3	52
Expected	12.1	6.9	26.2	6.7	
χ^2 Contribution	11.7	0.6	4	2.1	
Total	50	31	117	30	232

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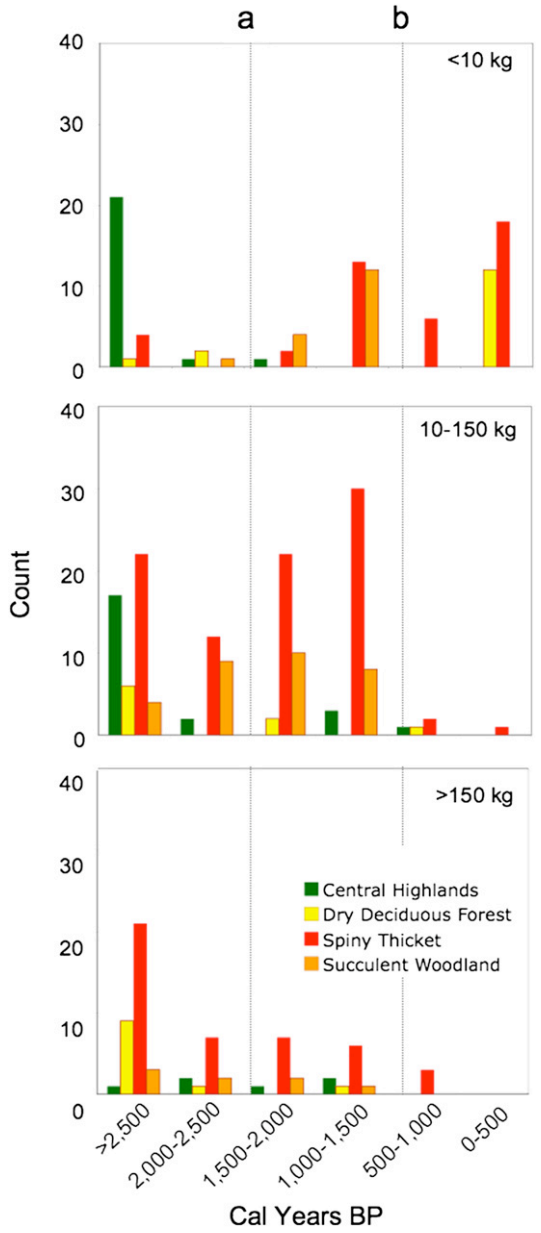

Fig. 4. Distribution of calibrated ^{14}C dates for very large, large, and small-to-medium-bodied animals in each ecoregion. Dashed lines indicate (a) the early period of decline by ca 2000 Cal BP, and (b) the more recent period decline of large animals in the southwest starting ca 1000 Cal BP.

endemic fauna between 2000 and 2500 Cal BP, predation by humans emerges as the most likely reason for this early wave of declines. Importantly, this pattern suggests that despite a lack of evidence for substantial anthropogenic activity beyond the southwest before 1300 Cal BP, humans may have had an early and profound impact on the fauna of the Central Highlands and Dry Deciduous Forest. Palynological records indicate that grasses were common in the Dry Deciduous Forest and Central Highlands, which suggests that these two ecoregions were not densely forested (e.g. MacPhee et al., 1985; Matsumoto and Burney, 1994; Gasse and Van Campo, 1998). Extinct animals would have spent their time in forest patches, or traveling across relatively open habitat (e.g. MacPhee et al., 1985), a lifestyle that would have made them easy targets for human hunters. Today, the Mikea, a little-known group of foragers who live in southwestern Madagascar, use dogs to hunt lemurs and the extant fossa (*Cryptoprocta ferox*) (Stiles, 1998). Similar to the Mikea, early human colonizers may have used dogs to hunt large extinct taxa. Although radiocarbon data for dogs do not lend support to this possibility, this may be due to small sample size; only a handful of radiocarbon dates exist for any introduced taxa.

Very large animals were impacted early in the southwest as well. Burney et al. (2003) suggested that the very large taxa (tortoises, elephant birds, and hippopotamuses) lived in relatively open areas in the Spiny Thicket and Succulent Woodland, again making them easy targets for human hunters. A decline in *Sporormiella* ca 1830 and 1560 Cal BP in the Spiny Thicket and Succulent Woodland, respectively, following the observed decline in these very large species by 2000 Cal BP agrees well with the suggestion that *Sporormiella* reflects the abundance of large herbivorous species (e.g. Burney et al., 2003). A subsequent increase in fire in the southwest between 1700 and 1500 Cal BP also fits within the proposed scenario that a decline in large herbivores such as elephant birds, hippopotamuses, and tortoises would have resulted in accumulated dried leaf litter, making the habitat more fire prone (Burney, 2003).

Large animals such as extinct lemurs in the arid southwest may have fared better than their counterparts in other regions because they were relatively protected by a harsh climate and inhospitable spiny scrub. Nevertheless, starting approximately 1000 Cal BP the number of large animals plummeted in the Spiny Thicket and Succulent Woodland ecoregions (Fig. 4; Table 5). The surge in fire frequency in the Spiny Thicket and Succulent Woodland ca 1700–1500 Cal BP cannot solely account for the decline in these species; increased charcoal levels predate the decline by several hundred years (Fig. 2) (Burney, 1987a,b, 1999; Matsumoto and Burney, 1994). It is possible but unlikely that competition with livestock could have negatively impacted remaining populations of extinct taxa (Dewar, 1997). No ^{14}C data exist for domestic livestock. Nevertheless, cattle remains in archaeological sites in the Central Highlands and Dry Deciduous Forest ca 1000 Cal BP (Wright and Rakotoarisoa, 1997), and *Sporormiella* increases recorded at Nosy Be off the coast of northwestern Madagascar (1025 $\pm$ 115 Cal BP) and at Lake Kavitaha in the Central Highlands (820 $\pm$ 150 Cal BP) indicate that livestock were abundant on the landscape at this time. Domestic species such as cattle and goats may have directly competed with remaining hippos, tortoises, and elephant birds, and they may have been partially responsible for the coincident island-wide shift towards more open vegetation (Burney, 1987a,b; Burney, 1993; Matsumoto and Burney, 1994; Virah-Sawmy et al., 2009). However, it is unlikely that grazing livestock directly competed with the large extinct lemurs of the southwest. Cattle were rare, if not absent from the southwest prior to ca 600 BP, when immigration caused the human population in the southwest to rapidly increase (Esoavelomandroso, 1995). Livestock populations likely remained small until the introduction of prickly pear cactus ca 250 Cal BP (reviewed in Kaufmann, 2004).

For over a millennium, large extinct lemur species persisted in the face of known hunting pressure in the southwest (Perez et al., 2003, 2005). Nevertheless, increasing human populations, or changes in hunting practices could have triggered a population crash in the large lemurs. Intensifying aridification between 2000 and 1000 Cal BP may have also played a role in the decline of the large extinct species in the southwest. Although all of the endemic species persisted through substantial climate and vegetation changes during the Pleistocene and Holocene, indirect and direct human pressures (e.g. increased reliance on bushmeat following crop failure, or human settlements near dwindling freshwater sources) would have lowered the ability of endemic taxa to recover from drought (Battistini, 1971; Mahé and Sourdat, 1972; Burney,

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1997; Goodman and Rakotozafy, 1997; Clarke et al., 2006; Virah-Sawmy et al., 2010). A coincident relative drop in sea level ca 1000–1400 Cal BP (possibly due to regional uplift) would have lowered the water table and further decreased the availability of freshwater, particularly in coastal habitats (Battistini, 1971; Camoin et al., 1997; Clarke et al., 2006; Virah-Sawmy et al., 2009).

The prolonged existence of large animals in the southwest after human arrival is perhaps surprising considering that the Spiny Thicket has yielded the oldest evidence for human-modified bones (MacPhee and Burney, 1991; Perez et al., 2003), and the most pronounced evidence for aridification (Burney, 1993). The extreme aridity in the southwest may have made it difficult for initial human colonizers to establish large settlements (Parker Pearson et al., 1995). Despite extensive surveying efforts in the southwest, no established settlements have been documented, and described archaeological sites have been limited to a few potsherds or cut bones (Battistini et al., 1963; MacPhee and Burney, 1991; Parker Pearson et al., 1995; Parker Pearson et al., 2002). It is uncertain when domestic species may have been introduced to the southwest, but aridity would have been a challenge for cattle as well. The introduction of fast-growing and water-filled prickly pear cactus (*Opuntia monocantha*) ca 250 Cal BP raised the carrying capacity of the southwest for both humans and cattle (Kaufmann, 2004).

Growing human populations have impacted the flora and fauna in the southwest, especially during the last century (reviewed in Kaufmann, 2004). Research suggests that even low levels of disturbance from cattle foraging and lumber harvesting for building materials can lead to forest loss because trees have low regeneration times (Sussman et al., 1994). If left unchecked, the same combination of factors that denuded the Central Highlands could spell disaster for the remaining flora and fauna of the Spiny Thicket and Succulent Woodland. Socioeconomic and cultural factors make an answer to this dilemma difficult. Nevertheless, history dictates that there is a need for greater awareness and involvement in conservation efforts by the local people.

5.2. Reliability of ^{14}C dates for tracing true species decline

The island-wide decline in radiocarbon dates for extinct species by 1000 Cal BP most likely reflects real population declines. Animals continued to be preserved in sediments younger than 1000 Cal BP (Fig. 3a), yet dated occurrences for extinct taxa more recent than 900 Cal BP are rare. Five extinct lemur species, hippopotamuses, giant tortoises, and elephant birds from across Madagascar have calibrated dates more recent than 900 Cal BP (Table 6). Yet only two extinct large species—*Megaladapis edwardsi* and *Palaeopropithecus ingens* both from Ankilitelo cave in the Spiny Thicket—have yielded dates close to European contact (585 ± 65 and 475 ± 155 Cal BP, respectively). Dates for these two individuals are substantially younger than late occurrence dates for other extinct species (Table 6). These relatively young dates support the suggestion that the Ankilitelo region may have provided a refuge for extinct species (Simons, 1997; Muldoon et al., 2009).

Table 6
Dated occurrences more recent than 1000 Cal BP for extinct taxa.

Taxon	Specimen no.	Ecoregion	Mean ^{14}C age	$\pm1\sigma$	Mean cal age	$\pm1\sigma$
Archaeolemur edwardsi	Not given	Dry Deciduous Forest	1020	50	870	90
Daubentonia robusta	UA 3890, Dr5	Spiny Thicket	1065	40	925	125
Megaladapis edwardsi	Not Given	Spiny Thicket	630	50	585	65
Megaladapis grandidieri	BM M 9927	Central Highlands	1035	50	875	95
Palaeopropithecus ingens	Not given	Spiny Thicket	510	80	475	155
Aepyornis sp.	Not given	Spiny Thicket	840	80	740	170
Hippopotamus sp.	Not given	Spiny Thicket	980	200	905	345
Geochelone sp.	MNHN 1884-30	Spiny Thicket	750	370	635	635

Despite the lack of fossil evidence, the probability that extinct very large and large animals survived until 1000 years ago is very high in all ecoregions except the Succulent Woodland (Table 7). However, with the exception of large animals from the Spiny Thicket, the probability that they persisted until 500 years ago is substantially less. In agreement with these patterns, colonial reports indicate that hippopotamuses, elephant birds, and perhaps *Palaeopropithecus* continued to exist, albeit in small numbers, until European contact (e.g. de Flacourt, 1661), and that hippos may have survived in isolated crater lakes into the late 1800s (Raybaud, 1902; Godfrey, 1986). Additionally, recent ethnographic accounts suggest that hippos, and possibly *Archaeolemur*, may have inhabited remote areas of the southwest into the last century (Burney and Ramilisonina, 1998). Nevertheless, these late-occurring species would have been very rare. Even with extensive exploration, European naturalists found no living examples of any extinct taxa. Thus these few ^{14}C dates and historical accounts do not contravene the conclusion that large taxa were rare, if not absent, long before European colonization.

It is important to note that although 50% confidence intervals give a better estimate than last dated occurrences for when each group went extinct, they say nothing about where within the 50% confidence interval the extinction happened. For example, there is a 50% chance that very large animals from the Central Highlands were gone by 818 Cal BP, but this event could have occurred anywhere between the last dated occurrence (1075 Cal BP) and 818 Cal BP (Table 7).

It is also important to remember that confidence intervals are only as accurate as the data upon which they are based. Large 50% CI for groups with small sample sizes (e.g. large animals in the Dry Deciduous Forest) indicates that we do not have a good estimate on when they became extinct.

Dated occurrences for small-to-medium-bodied extant taxa were infrequent until ca 1000 Cal BP. This observed pattern could have resulted from biases in post-burial preservation (smaller bones were more easily fragmented and crushed than large bones), sample collection (small bones were overlooked), or sample selection for radiometric dating (research focused on extinct species). Yet the relatively consistent number of small-to-medium-bodied taxa across time bins suggests that the increase in dates for smaller-bodied species in more recent years primarily reflects the decline of larger-bodied taxa. The absence of recent dated occurrences for small-to-medium-bodied taxa from the Succulent Woodlands and the Central Highlands presents an exception to this pattern. There are two alternative explanations for these observed trends: 1) small-to-medium-bodied animals persisted, but were not dated, or 2) small-to-medium-bodied animals declined with their larger counterparts.

Today, small-to-medium-bodied species continue to thrive in the Succulent Woodland, and the lack of recent dates for these species is likely an artifact of sampling bias. Conversely, it is probable that small-bodied taxa declined along with the larger taxa in the Central Highlands. Aside from a few isolated forest fragments, this ecoregion is currently covered by vast expanses of grassland that are burned annually (Duplantier and Duchemin, 2003), and extant endemic species are largely absent from this ecoregion today. Unfortunately, ^{14}C dates do not definitively answer this question. Radiocarbon dates suggest that both small and large species declined by 2000 Cal BP in the Central Highlands (Table 7).

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Table 7
Number of dated specimens <4000 Cal BP, most recent ^{14}C dates, 50% confidence intervals, and probabilities that each mass group in each ecoregion was present 1000 or 500 Cal BP, or could still be around today. Island totals for large and very large animals include two *Megaladapis* with unknown provenience, and a *Hippopotamus* from the Humid Forest, respectively.

Group	Ecoregion	*N*	Youngest date	Size of 50% CI	Upper 50% CI	Probability present 1000 Cal BP	Probability present 500 Cal BP	Probability present today
<10 kg	Central Highlands	10	1810	157.7	1652.3	0.05	0.01	0.00
<10 kg	Dry Deciduous Forest	14	225	110.9	114.1	1.00	1.00	0.25
<10 kg	Spiny Thicket	41	0	50.4	0.0	1.00	1.00	1.00
<10 kg	Succulent Woodland	17	1065	42.3	1022.7	0.35	0.00	0.00
<10 kg	Island-wide	82	9	32.4	0.0	1.00	1.00	1.00
10–150 kg	Central Highlands	8	875	216.5	658.5	1.00	0.31	0.09
10–150 kg	Dry Deciduous Forest	5	870	376.5	493.5	1.00	0.51	0.23
10–150 kg	Spiny Thicket	84	475	26.1	448.9	1.00	1.00	0.00
10–150 kg	Succulent Woodland	30	1100	65.3	1034.7	0.35	0.00	0.00
10–150 kg	Island-wide	129	475	18.1	456.9	1.00	1.00	0.00
>150 kg	Central Highlands	5	1075	257.3	817.7	0.81	0.24	0.10
>150 kg	Dry Deciduous Forest	6	1025	395.5	629.5	0.95	0.41	0.20
>150 kg	Spiny Thicket	36	635	56.4	578.6	1.00	0.19	0.00
>150 kg	Succulent Woodland	8	1135	178.0	957.0	0.59	0.11	0.03
>150 kg	Island-wide	56	635	38.7	596.3	1.00	0.09	0.00

It is, however, difficult to believe that early human hunters would have eradicated small-to-medium-bodied species. It is more likely that the smaller species declined more recently than carbon dates indicate and that taphonomic or sample bias accounts for the lack of carbon dates more recent than ca 2000 Cal BP. In addition to hunting pressures, an increase in frequently burned grasses at the expense of woody vegetation commencing ca 1400 BP, and competition with introduced livestock commencing ca 1000 BP would have reduced resources for both large and small-to-medium-bodied species (Burney, 1987a,b; Burney et al., 2003; Duplantier and Duchemin, 2003). Today, the limited fauna remaining in the Central Highlands is threatened by continued habitat destruction.

5.3. Using ^{14}C dates to infer locality-specific chronologies

The potential for using ^{14}C dates to predict the chronologies of individual subfossil localities is alluring. At present, however, the utility of using ^{14}C dates from subfossil bones for these purposes is unfortunately minimal. The majority of the most prolific subfossil localities (e.g. Ampasambazimba, Andrahomana, Taolambiby, and Tsirave) were excavated in the late 1800s and early 1900s, before the usefulness of carefully recorded excavations was recognized. The precise location of some of these subfossil localities is completely unknown. Some localities have been revisited, only to find that they have been flooded or are under fields (e.g. Amparihingidro and Taolambiby, L.R. Godfrey, personal communication). Other localities have been revisited, and stratigraphic sections have been sampled (e.g. MacPhee et al., 1985; Burney, 1993; Burney et al., 2003). Although these sections are very valuable for reconstructing regional histories, direct comparisons between these sections and the dated subfossil bones are difficult for two reasons: (1) without knowing where subfossils were originally excavated, it is difficult to reconstruct a stratigraphic context for the bones that are in museum collections (the majority of the bones that have been dated), and (2) the majority of the sections were taken near the subfossil localities because the actual localities have very little stratigraphic integrity (e.g. Ampasambazimba and Anjohibe, MacPhee et al., 1985; Matsumoto and Burney, 1994). Dates on stratigraphic sections from the Ampasambazimba region range from ca 5325 to 9050 Cal BP (MacPhee et al., 1985), which is substantially less than the range in subfossil vertebrates (ca 870 Cal BP to 29 240 ^{14}C BP) (Appendix A). Dates from a stratigraphic section bracketing bone-bearing layers at Ambolisatra (ca 1760–5605 Cal BP, Burney, 1993) are more similar to the range in dates for subfossil bones from this locality (ca 635–5935 Cal BP, Appendix A), but the dates still differ by over 1000 years during a critical period in the Late Holocene. Pinpointing the stratigraphy of Andrahomana, a coastal cave in southeastern Madagascar, may be possible in the future. However, even the relatively obvious stratigraphic layers at this locality show evidence for mixing (Burney et al., 2008). Radiocarbon dates for specimens included in this manuscript do not shed light on the stratigrapahic integrity of this locality. Whereas surficial specimens do, indeed, have young dates ranging from modern to 485 Cal BP (Appendix A), the stratigraphic context for older specimens is unknown.

Despite the lack of stratigraphic context, there are patterns in which types of localities tend to preserve older and younger bone. With the exception of an eggshell that was considered too old to produce a ^{14}C date from the Spiny Thicket (Clarke et al., 2006), the paleolakes/wetlands of the Central Highlands (e.g. Ampasambazimba and Antsirabe) preserve the oldest dated subfossils, but lack dates more recent than ca 1000 Cal BP (Fig. 5). Inland caves preserve both some of the oldest and some of the youngest subfossil material. Dates from coastal caves are slightly younger

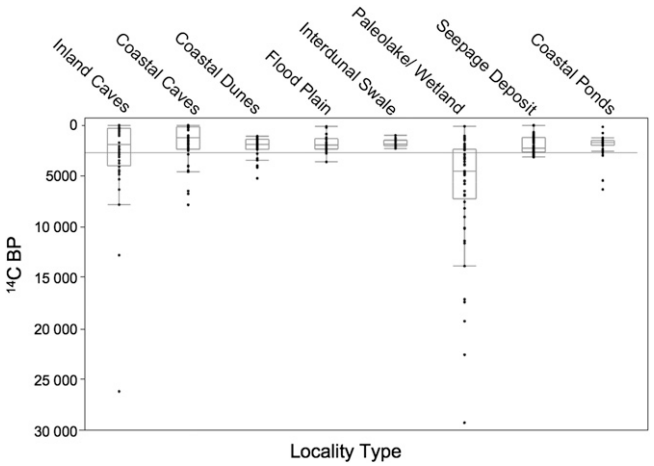

Fig. 5. Distribution of ^{14}C dates (uncalibrated) for each locality type. Horizontal line represents the grand mean for all localities (2659 ^{14}C BP). All coastal bodies of water are lumped into the "coastal pond" category. Bemaraha is included in the "inland cave" category, and Tsirave is included in the "flood plain" category. An eggshell from *Aepyornis* sp. deemed too old to carbon date (Clarke et al., 2006) was not included.

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than those at inland caves. With the exception of a few older individuals, dates from coastal dunes, interdunal swale, coastal ponds, seepage deposits, and flood plains all represent a relatively small window of time ca 2000–1000 Cal BP (Fig. 5). I acknowledge that some of these patterns may result from preservation biases, and I attempted to date several dozen of bones without success. Bones from Anjohibe, Andrahomana, and Ampasambazimba were particularly prone to not yielding ^{14}C dates, and it is possible that these specimens were simply too old to date.

6. Conclusions

Here I have revisited the Late Holocene history of Madagascar's megafauna. Although these dates do not clarify precisely when these species went extinct, clear patterns in species decline have emerged. Within 500 years after human colonization ca 2500 Cal BP, populations of very large and large species declined in the Dry Deciduous Forest, and populations of large and small-to-medium-bodied species declined in the Central Highlands. Populations of very large species were also impacted in the Spiny Thicket. These declines most likely resulted from human predation and suggest that humans affected the ecologies of the endemic vertebrate communities before the establishment of substantial human settlements, vegetation transformation, or increased fire frequency (Burney, 1987a,b; Burney, 1993; Matsumoto and Burney, 1994; Burney et al., 2003; Virah-Sawmy et al., 2009). Large extinct taxa persisted in the Spiny Thicket and Succulent Woodland until at least ca 1000 Cal BP. Population declines in these species likely resulted from a combination of continued hunting pressure, habitat reduction and transformation, and climatic desiccation. Unfortunately the very same anthropogenic effects that are thought to have led to the demise of the extinct taxa continue their assault across the island today (Favre, 1996; Richard and O'Conner, 1997; Stiles, 1998; Goodman and Raselimanana, 2003; Godfrey and Irwin, 2007; Golden, 2009). The paucity of lemurs in the Central Highlands attests to the vulnerability of extant lemur populations. Although populations of small-to-medium-bodied extant taxa increased over the last millennium, particularly in the last 500 years, persistent hunting pressure and habitat reduction combined with an uncertain climate may very well spell disaster for the remaining extant taxa. Continued conservation and education efforts will be vital to the persistence of Madagascar's remaining biodiversity.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.quascirev.2010.06.030.

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